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NOTE

Sneaker Males Affect Fighter Male Body Size and Sexual Size Dimorphism in Salmon

Laura K. Weir,^{1,2,*} Holly K. Kindsvater,^{3,4} Kyle A. Young,⁵ and John D. Reynolds^{3,†}

1. Department of Biology, Saint Mary's University, 923 Robie Street, Halifax, Nova Scotia B3H 3C3, Canada; 2. Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4, Canada; 3. Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada; 4. Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, New Jersey 08901; 5. Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

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ABSTRACT: Large male body size is typically favored by directional sexual selection through competition for mates. However, alternative male life-history phenotypes, such as “sneakers,” should decrease the strength of sexual selection acting on body size of large “fighter” males. We tested this prediction with salmon species; in southern populations, where sneakers are common, fighter males should be smaller than in northern populations, where sneakers are rare, leading to geographical clines in sexual size dimorphism (SSD). Consistent with our prediction, fighter male body size and SSD (fighter male:female size) increase with latitude in species with sneaker males (Atlantic salmon *Salmo salar* and masu salmon *Oncorhynchus masou*) but not in species without sneakers (chum salmon *Oncorhynchus keta* and pink salmon *Oncorhynchus gorbuscha*). This is the first evidence that sneaker males affect SSD across populations and species, and it suggests that alternative male mating strategies may shape the evolution of body size.

Keywords: alternative mating strategies, competition, latitudinal clines, salmonids, sexual selection.

Introduction

Both natural and sexual selection can influence the magnitude and direction of sexual size dimorphism (SSD) between males and females. In general, large body size in females is favored by fecundity selection, whereas large size in males is often favored by sexual selection through male-male competition or female preference for larger males (Andersson 1994; Fairbairn 1997). Variation in SSD thus provides evidence for variation in the type and strength of selection acting on male and female body size (Fairbairn

1997). For example, all else being equal, male body size and male-biased SSD are expected to increase with the intensity of intrasexual competition among males.

Evidence from a range of taxa confirms that variation in the strength of sexual selection on male body size drives variation in SSD (Fairbairn 1997). Despite their occurrence in many animal species (Oliveira et al. 2008), the influence of alternative male reproductive tactics, like “sneaking,” on male body size and SSD remains unexplored. The effect of sneaker males on the evolution of SSD likely varies across mating systems (Jones et al. 2001). In primarily monogamous systems, extrapair fertilizations may increase the opportunity for sexual selection on male body size by increasing the variance in male reproductive fitness. However, in polygamous systems, the addition of sneaker males is expected to reduce male mating skew and the opportunity for sexual selection. If mating skew results from size-dependent male competition, small sneaker males should reduce the relative fitness of all large “fighter” males or decrease the strength of directional selection on fighter male body size if larger fighter males disproportionately lose copulations to sneakers. These nonexclusive mechanisms lead to the common prediction that fighter males will be smaller in populations with sneaker males than in populations without sneaker males, such that SSD will be less pronounced or even female biased (Neff 2001).

Anadromous salmonids are fish that mature in the ocean before returning to freshwater to reproduce. For a number of reasons, this group is ideal for testing the prediction that sneaker males decrease fighter male body size. First, the duration of the marine growth phase—the principal determinant of adult body size—varies markedly within and between sexes, populations, and species (Groot and Margolis 1991), providing evolutionary scope for SSD to vary across levels of biological organization (Young 2005). Due

* Corresponding author; e-mail: laura.weir@smu.ca.

† ORCID: Kindsvater, <http://orcid.org/0000-0001-7580-4095>.

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to the influence of the marine environment on body size, there is a strong advantage of ocean migration for females because of increased fecundity, and thus females are typically anadromous. Large size in males is associated with dominance during mating, and their aggressive behavior categorizes anadromous males as fighters (Gross 1984; Fleming 1998). Second, the mating system of salmonids is characterized as contest competition polygynandry (Andersson 1994), whereby fighter males engage in contest competition for access to breeding females and display strong reproductive skew, both sexes can have multiple mates over a breeding season, and sexual selection favors large body size for both males and females (Fleming 1998). Third, in some species, males can also mature as freshwater “parr” without migrating to sea. These mature parr are an order of magnitude smaller than anadromous males and females (Jones 1959; Hutchings and Myers 1988). Mature male parr gain access to breeding females by sneaking rather than fighting and are thus categorized as sneakers. Parr maturation rate varies across populations and is under both genetic and environmental control (Piché et al. 2008; Morita and Nagasawa 2010). The incidence of sneaker males typically decreases with latitude, because lower temperatures and shorter growing seasons prevent juveniles from reaching the size at which early maturity is favorable (Baum et al. 2004; Valiente et al. 2005; Morita and Nagasawa 2010). Fourth, in some species, all males are anadromous and adopt the fighter strategy during breeding (Groot and Margolis 1991). The salmonid clade thus provides the key elements required to test the prediction that sneaker males alter sexual selection on fighter male body size and influence the evolution of SSD: variation in fighter male body size and anadromous SSD (fighter male:female body size) among populations and species; evidence for directional sexual selection on fighter male body size; intraspecific variation in the frequency of sneaker males; and “control” species, in which only the anadromous fighter male phenotype occurs.

Here, we examine the relationship between sneaker frequency, measured as the incidence of parr maturity, and interpopulation variation in fighter male body size and anadromous SSD. Because data for sneaker frequency and anadromous male and female body size from the same populations were not available, we took advantage of well-documented latitudinal clines in sneaker male frequency (Baum et al. 2004; Valiente et al. 2005; Morita and Nagasawa 2010). The latitudinal decreases in sneaker male frequency give rise to two complementary geographical predictions: (1) among populations of species with sneaker males, fighter male body size and anadromous SSD (fighter male:female body size) should increase with latitude; (2) among populations of species without sneaker males, neither fighter male body size nor anadromous SSD should increase systematically with latitude.

Methods

Species with Alternative Male Mating Strategies

To test the first prediction, that fighter male body size and anadromous SSD increase with latitude in species with alternative male mating strategies, we collected data on anadromous fish body size and the frequency of sneakers, or mature male parr, for populations from different latitudes for two species with male parr maturation: Atlantic salmon (*Salmo salar*) and masu salmon (*Oncorhynchus masou*; tables A1, A2, available online). Latitude was treated as a “common factor” for parr maturation frequency and anadromous body size, because data for both variables were rarely available from the same population (both types of data were available for only one population in each species). We were not able to acquire sufficient data for other species with both fighter and sneaker males (e.g., rainbow or steelhead trout *Oncorhynchus mykiss*).

Data for Atlantic salmon parr maturation rates were taken from a review of latitudinal variation in life history (Valiente et al. 2005). Anadromous fish body size data for 15 rivers over multiple years in the Canadian Maritimes and Newfoundland were obtained from stock reports or the Department of Fisheries and Oceans, Canada. Unpublished size data for Catamaran Brook, New Brunswick, Canada, were obtained from R. A. Cunjak (University of New Brunswick). Anadromous fish are captured during their upstream migration at counting fences and measured before being released. All anadromous fish data included the average size of males and females in any given year as well as the sample size for each sex. We calculated the mean male and female body size for each river over all years. Most of the data for Atlantic salmon come from rivers in Newfoundland where anadromous fish return after 1 year at sea; thus, anadromous SSD results from sex differences in marine growth rates rather than marine age at maturity. Because Atlantic salmon are iteroparous, we included body size data from only those Atlantic salmon that were returning to spawn for the first time to avoid confounding variation in sex-specific rates of iteroparity with variation in SSD. Masu salmon data were obtained from published studies on latitudinal variation in male parr maturity (Morita and Nagasawa 2010) and anadromous male and female body size (Tamate and Maekawa 2006).

Species without Alternative Male Mating Strategies

To test our second prediction, that neither male body size nor SSD should increase with latitude in species without alternative male strategies, we collected body size data from populations of two species that lack the sneaker male phenotype: chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*; table A2). Data were collected by one of us (K.A.Y.) using methods reported

elsewhere (Young 2005). For each population, we again calculated mean male and female body size across years. Both species are semelparous; thus, all fish were included in the analyses. All pink salmon mature after 2 years at sea; SSD thus results from sex differences in marine growth rate. Chum salmon mature at various marine ages, so SSD in this species results from sex differences in both marine growth rate and age.

Data Analysis

We used the ratio of fighter male:female body size as our measure of anadromous SSD (Young 2005; Tamate and Mae-kawa 2006). All data were analyzed using linear mixed-effects models with latitude as a fixed effect and species as a random effect. Using this approach, we first tested earlier findings that the incidence of male parr maturity decreases with latitude in Atlantic and masu salmon.

Due to the geographical context of our predictions, our main objective was to test whether latitude was a significant predictor of fighter male (but not female) body size and anadromous SSD and whether this pattern differed for species with and without sneaker males. We thus constructed models that contained an interaction between latitude and presence or absence of sneakers for measures of anadromous body size, and we compared these interactive models to additive models as well as models with only one predictor (either latitude or presence or absence of sneakers). To determine which model best explained the data, we used the Akaike information criterion (AIC) value for each model corrected for sample size (AICc). The “best” model was the model that had the lowest AICc by a value of 2 or greater. Because the direction of the latitudinal trend affects our interpretation of the results, we also report the estimates of the latitudinal effects and their significance within pairs of species with or without male parr maturation. Models were fitted using maximum likelihood to allow for comparison of fixed effects. All analyses were conducted using the lme4 package (Bates et al. 2015) in R (ver. 3.1.1; R Core Team 2015). All data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.76rd1> (Weir et al. 2016).

Results

As expected, the frequency of male parr maturation decreased with latitude across populations of Atlantic and masu salmon (tables 1, 2; fig. 1A, 1B). We found a significant interaction between latitude and the presence or absence of alternative male mating phenotypes for both fighter male body size and anadromous SSD but not for female body size (table 1). Because of the significant interactions, we also analyzed our data within pairs of species with or without alter-

Table 1: Summary of linear mixed effects models

Dependent variable, model	AICc	Δ AICc	ω_i
Proportion mature male parr:			
Latitude	10.2	0	1.00
Intercept only	21.8	11.6	.00
Male body size:			
Latitude \times alternative strategy	734.2	0	1.00
Latitude + alternative strategy	772.0	37.8	.00
Alternative strategy	772.5	38.3	.00
Latitude	776.4	42.2	.00
Intercept only	776.7	42.5	.00
Female body size:			
Alternative strategy	626.7	0	.71
Latitude \times alternative strategy	629.8	3.1	.15
Intercept only	631.1	4.4	.08
Latitude + alternative strategy	631.6	4.9	.06
Latitude	636.0	9.3	.01
Sexual size dimorphism:			
Latitude \times alternative strategy	-457.4	0	1.00
Intercept only	-431.9	25.6	.00
Alternative strategy	-428.4	29.0	.00
Latitude	-428.0	29.4	.00
Latitude + alternative strategy	-420.9	36.5	.00

Note: Models specified as “latitude \times alternative strategy” are full factorial models, whereas models defined as “latitude + alternative strategy” do not include an interaction between the two fixed factors. Similarly, models described by only one fixed factor include only that factor, whereas models designated simply as “intercept” contain no fixed factors. AICc = Akaike information criterion for a particular model corrected for small sample size; Δ AICc = difference between a given model and the model with the smallest AICc; ω_i = relative weight of each model.

native male mating strategies to determine the magnitude and direction of the latitudinal effects on anadromous fish body size and SSD.

In species with sneaker males, fighter male body size increased with latitude, while there was no trend in female body size (table 2; fig. 1C–1F). This resulted in an increase in anadromous SSD with latitude (table 2; fig. 1G, 1H). These patterns support our geographic prediction that fighter male body size, and thus anadromous SSD, should increase with latitude due to a decrease in the frequency of sneaker males.

In species without sneaker males, male body size and anadromous SSD decreased slightly with latitude, with no latitudinal trend in female size (table 2; fig. 2). These latitudinal trends in male body size and SSD are opposite to those observed in species where precocious parr maturation occurs, thus supporting our hypothesis that sneaker males reduce the strength of sexual selection on fighter male body size.

Discussion

Our data from populations of four salmon species support the prediction that sneaker males can reduce the strength of

Table 2: Estimates of the latitudinal effect, its standard error (SE), the significance from mixed-effects models, and the marginal R^2 value within pairs of species with or without alternative mating strategies

Species mating strategy, dependent variable	Latitudinal effect			
	Coefficient	SE	P	R^2
Species with alternative mating strategies:				
Proportion mature male parr	-.10	.02	<.001	.49
Male body size	14.7	2.9	<.001	.36
Female body size	2.6	1.7	.12	.06
SSD	.022	.004	<.001	.50
Species without alternative male mating strategies:				
Male body size	-3.9	1.5	.011	.06
Female body size	-1.3	1.1	.23	.0008
SSD	-.005	.002	.004	.08

Note: These models include latitude as a fixed effect and species as a random effect and are constructed within each alternative strategy category (i.e., presence or absence of mature male parr) to test for any interactive effects from the full models and to examine the direction of the latitudinal effect for each dependent variable. SSD = sexual size dimorphism.

sexual selection on fighter male body size, resulting in reduced fighter male body size and anadromous SSD. In the two species with alternative male life histories, anadromous fish SSD changes from female biased at low latitudes, where sneakers are common, to male biased at high latitudes, where sneaker males are rare. Importantly, for both species, the latitudinal increase in SSD is driven by marked increases in fighter male body size only, whereas female body size varies little with latitude. By contrast, there was a negative relationship between latitude and male body size and SSD in species without the sneaker phenotype. Taken together, these results support our hypothesis that alternative sneaker male strategies affect the evolution of fighter male body size and anadromous SSD.

We suggest that our results are best explained by latitudinal variation in the frequency of sneaker males in species with parr maturation (Valiente et al. 2005; Morita and Nagasawa 2010). While latitudinal increases in body size are common among ectotherms (Lindsey 1966; Blanckenhorn et al. 2006), our data suggest this pattern does not hold in anadromous salmon. Fighter male Atlantic and masu salmon were larger at high latitudes, but there was no such trend for females, nor for species without alternative male strategies. An alternative explanation for the patterns observed in fighter male body size could be an increase in population size and spawning density with latitude (where habitats are less impacted by humans), leading to density-dependent sexual selection for larger body size in fighter males but not in females (Tamate and Maekawa 2006). While this explanation would be consistent with patterns observed in the species with parr maturation, it is inconsistent with the patterns observed in species without sneaker life histories. It is also possible that sneakers may relax selection on the size of fighter males through an indirect mechanism. The presence of sneaker males should reduce the frequency of fighter males in a population, given

that the two male phenotypes represent a mixed evolutionarily stable strategy (Hutchings and Myers 1988). The associated decrease in fighter male density could relax density-dependent selection for size by reducing the intensity of competitive interactions among fighter males.

While sexual selection can partially explain variation in fighter male body size across populations, anadromous salmonid body size is principally determined by the amount of time spent in the marine environment before sexual maturity (Young 2005; Sloat et al. 2014). Variation in marine age may contribute to the body size patterns that we observed in this study, but it does not contradict the role of alternative male strategies in driving variation in anadromous male body size. Rather, our findings suggest that the presence of sneaker males may alter the nature of selection on marine maturation age by changing the form or strength of sexual selection on fighter male body size. Our data also suggest that the presence of sneaker males may affect fighter male body size by influencing growth rates in the marine environment; we observed a positive latitudinal relationship for fighter male body size in Newfoundland populations of Atlantic salmon, despite the fact that all fish included in our data set spent the same amount of time (1 year) growing in the marine environment. While this pattern could be explained by the fact that, at low latitudes, faster-growing males mature as sneakers and remain in freshwater, thereby leaving the slower-growing males to go to sea, there is no evidence for a strong correlation between freshwater and seawater growth rates in anadromous salmonids (Johnsson et al. 1997), which makes this explanation unlikely.

Because males that mature as sneakers do not suffer mortality associated with anadromy, they can significantly alter the male-to-female operational sex ratio (OSR; Emlen 1976) by increasing the number of reproductively active males. Experimental (Thomaz et al. 1997; Jones and Hutchings 2001,

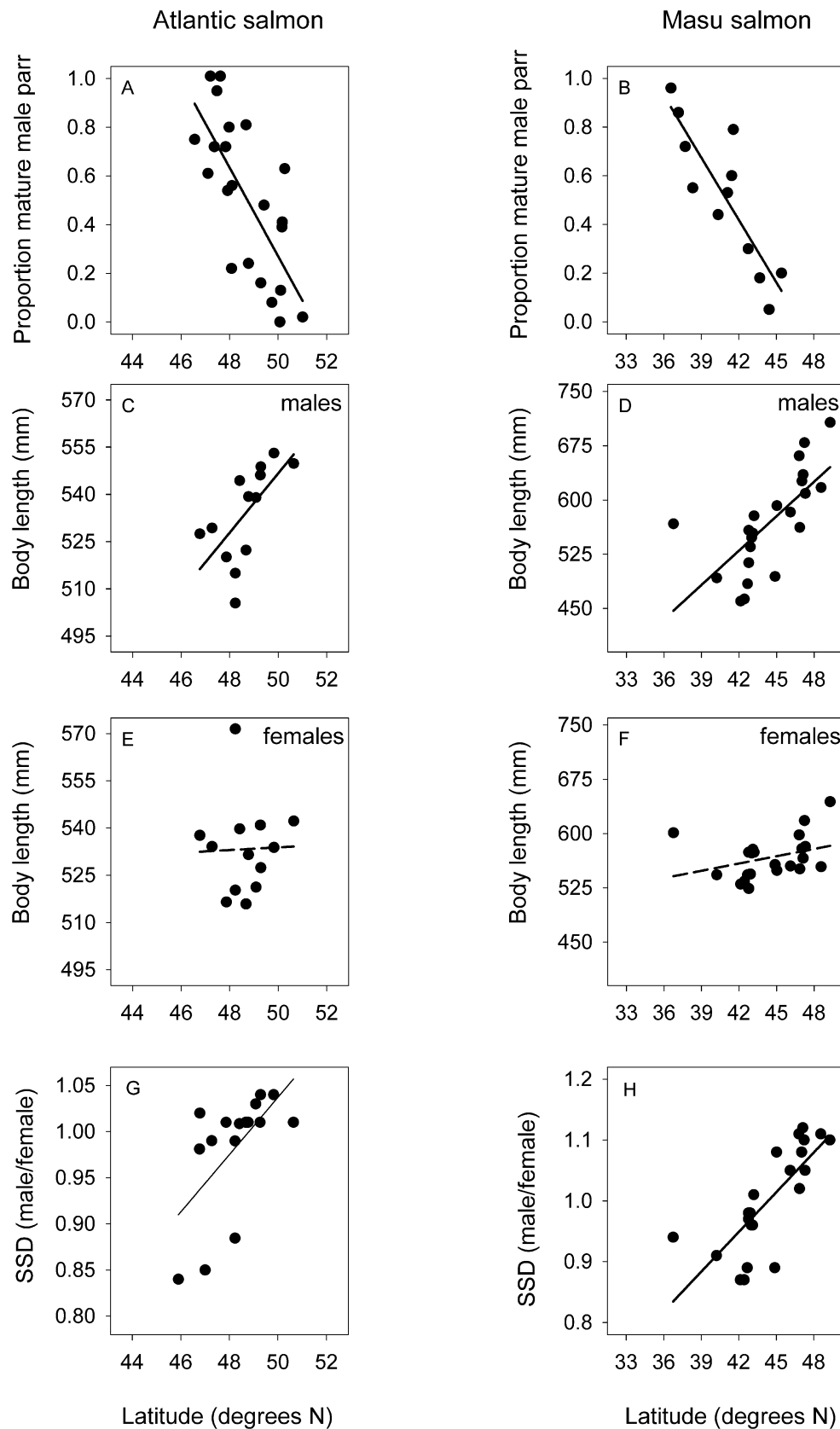


Figure 1: Latitudinal trends in proportion of mature parr sneaker males (A, B), fighter male size (C, D), anadromous female size (E, F), and fighter male:female sexual size dimorphism (SSD; G, H) for salmonid species with the sneaker male phenotype. Solid lines indicate significant latitudinal trends among populations; dashed lines indicate nonsignificant trends. Outliers for SSD in Atlantic salmon are from three rivers in the Maritime region of Canada, where anadromous fish may remain at sea for 1 or 2 years before returning to the river to spawn. In these cases, females often remain at sea for 2 years and return at a much larger size, thus influencing SSD for these rivers. Excluding these rivers from our analysis did not affect the interpretation of our results.

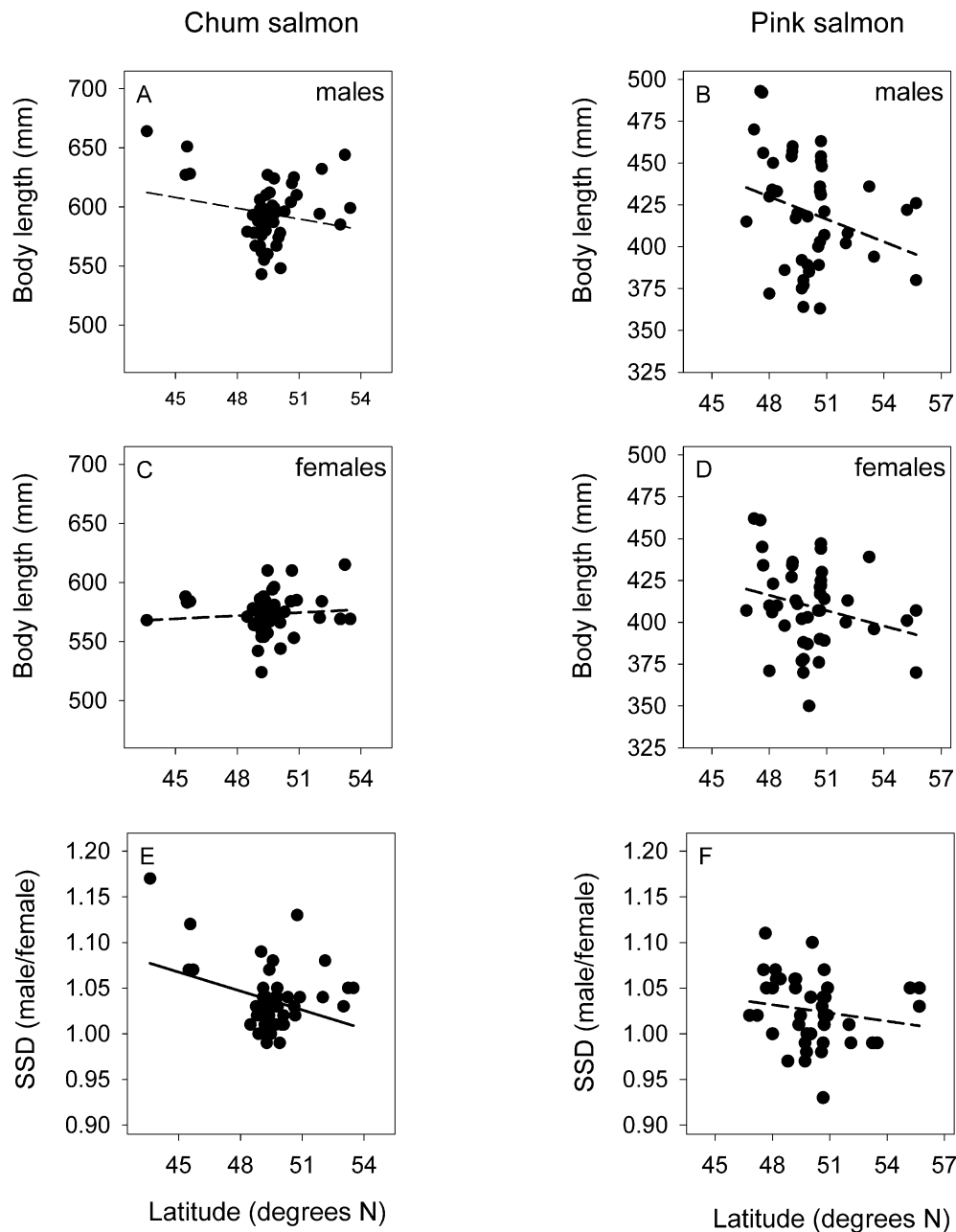


Figure 2: Latitudinal trends in male size (A, B), female size (C, D), and sexual size dimorphism (SSD; E, F) for salmonid species without the sneaker male phenotype. Solid lines indicate significant latitudinal trends among populations; dashed lines indicate nonsignificant trends.

2002; Garant et al. 2003; Berejikian et al. 2010) and observational (Taggart et al. 2001; Weir et al. 2010; Richard et al. 2013) evidence demonstrates that sneaker males can have high reproductive success and significantly increase the effective size (N_e) of populations (L'Abée-Lund 1989; Valiente et al. 2005). Theory predicts that increases in OSR should increase the strength of selection on male body size and secondary sexual traits (Andersson 1994; Reynolds 1996), and variation in OSR has been invoked to explain variation in fighter

male body size among salmon populations (Quinn 1999; Tamate and Maekawa 2006). The finding that fighter males are smaller in populations where the OSR is highly male biased due to the presence of sneaker males suggests that OSR alone is insufficient to explain variation in SSD among populations or species with alternative male mating strategies.

It is possible that genetic correlations between alternative male phenotypes could influence patterns in fighter male body size. If so, this would imply that opposing forces that

select for small size in sneakers may constrain the evolution of large size in fighters. This type of antagonistic interaction can occur between alternative male morphs, as well as between males and females when their respective fitness optima for a particular trait differ (Morris et al. 2013; Buzatto et al. 2015). However, we do not think this drives the patterns observed in our study, for two reasons. First, empirical evidence from both Atlantic salmon (Thomaz et al. 1997) and masu salmon (Koseki and Maekawa 2000) suggests that large size is advantageous for sneakers, because body size correlates with fertilization success and dominance among mature male parr. Second, there is no evidence for correlated changes in female body size, which does not vary with mature parr frequency.

This study documents a strong geographical relationship between the frequency of mature parr, fighter male body size, and anadromous SSD across populations of two salmonid species. A mechanistic role for sneaker males in driving variation in anadromous male size and SSD is further supported by the fact that the two species lacking alternative male mating strategies do not exhibit similar latitudinal patterns. Precocious male parr maturation appears to be an ancestral trait that is almost exclusively associated with iteroparity among the anadromous branches of the salmonid phylogeny (Crespi and Teo 2002; but see Unwin et al. 1999 for an exception in hatchery fish). While anadromous males in some semelparous *Oncorhynchus* species can mature as “jacks” after a few months in the sea and adopt a sneaking strategy, alternative male mating phenotypes are not present in the most recently diverged *Oncorhynchus* clade, which includes pink and chum salmon (Esteve and McLennan 2007; Crête-Lafrenière et al. 2012). Although our small sample size (four species) precludes informative comparative phylogenetic analyses, the fact that masu salmon is more closely related to pink and chum than to Atlantic salmon suggests that the patterns we observe are not artifacts of phylogenetic history.

Our results are consistent with the hypothesis that sneaker males can affect the evolution of fighter male body size and anadromous SSD, and they offer a new explanation for variation in fighter male size and anadromous SSD in salmon. More generally, this study highlights the potentially important role of alternative male mating strategies in determining the relationship between sexual selection, the evolution of body size, and sexual size dimorphism across populations and species.

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